Fitness — scalar or vector?[1]

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In population genetics, fitness is ordinarily regarded as the expected relative number of offspring (or other units) in the next generation. This view works pretty well for the kinds of organisms and levels of processes that are commonly considered in that field.

It does, though, break down in several ways in a broader context. I've discussed those that I recognized (Van Valen, 1989) and am revisiting the subject in a book in progress. Here I focus on time scales.

When time scales are recognized to be a problem in population genetics, this is most often exemplified by the mutation *grandchildless* in *Drosophila subobscura* (Spurway, 1949; Suley, 1953). Crossing of homozygotes produces offspring of perhaps normal viability. These offspring are, however, sterile, so there are no second-generation offspring. (Stock cultures of *grandchildless* were therefore difficult to maintain, as this had to be done by progeny-testing for heterozygotes.) Similar mutations have since been found in other animals.

So a *grandchildless* homozygote has a relative fitness of perhaps 1 over one generation but 0 over two generations. What is its overall fitness?

On a different scale, the geneticist Thoday (1953) noted that one shouldn't stop consideration so soon and proposed that fitness be taken, ontically, over an interval such as 10^8 years. Such an interval presents a certain epistemic awkwardness for geneticists. Moreover, why not 10^9 years, or 10^6?

Paleontologists are comfortable with such time scales, though, and sometimes study the effects of natural selection, on supraspecific units, over such intervals. Estimates of fitness thereby emerge for the units considered. However, such estimates are not invariant over time. The initiator of the trilobite clade had a positive fitness until the clade became extinct in the Permian; over longer intervals we estimate its fitness as 0. What, specifically, was its overall fitness?

Is the overall fitness of an extant clade indeterminate ontically or only epistemically? And one can go on with similar questions.

One might want to use a weighting function so that shorter intervals are seen as more important than longer ones. I once

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tentatively suggested using an exponentially declining function (Van Valen, 1973). But what exponent? Why exponentiality anyway rather than some other function? There is no natural analog to the economists' discount rate.

More importantly, fitness is something which plays an important causal role in the real world. It isn't something which we can adjust to suit our personal predilections or aesthetic tastes.

So. How, then does fitness participate in causal processes at different time scales?

Fitness being an expectation in the statistical sense, more specifically a propensity, one can't just look retrospectively at what happened. What we estimate that way is called realized fitness, and it is ordinarily our best estimator of fitness itself, but it's a result rather than a cause. Nonselective processes can also participate in the result and even overwhelm any selective participation.

The fitness of an allele, or of a clade's initiator, or of any other unit of selection, must depend on the properties of the unit at the beginning of the interval we are considering. (The fitness may of course change over time, and commonly does, but that is quite a different matter conceptually from the initial fitness despite causal overlap.) Relative fitness involves a net comparison with the properties of some other unit or units at the same time, each in its own environmental context.

At any point in time, how an evolutionary unit can contribute to the future depends on its realized fitness at that point. For instance, if it no longer survives it can contribute nothing even if it would do quite well if it had survived.

Just as for a single generation, the initial properties of the evolutionary unit interact with the actual later environment to produce an outcome in evolutionary space.[1]

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[1]Because future events are unpredictable in detail, and progressively more so over longer intervals of time, it may be tempting to consider, somehow, all possible environments. However, even apart from its empirical possibility, such a choice ignores the fact that there will be only one real future, in which some range of environments (sensu latissimo) will be experienced contemporaneously.

Similarly, fitness varies with environment even contemporaneously, so one might want to argue in the same way for a higher-dimensional array to express fitness.

The problem in such approaches is that the actual fitness gets confused with its estimation. The actual fitness is real, ontic, causal. Its estimate is hypothetical, epistemic, and only potentially causal.

Nevertheless, both the real fitness and its estimate have the same basic structure. For every future interval or instant, there is a single fitness value (or best value, for the estimate.) Therefore fitness is a vector rather than a scalar. Moreover, because real time is continuous (the Planck scale being irrelevant), the vector for at least real fitness is also continuous in the sense that it can change (continuously or discretely) at any point in time, its variation not being restricted to predefined intervals.

Therefore fitness is a continuous vector over time.

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